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UNITED STATES DEPARTMENT OF AGRICULTURE

BULLETIN No. 542

Contribution from the Bureau of Plant Industry
WM. A. TAYLOR, Chief

Washington, D. C. PROFESSIONAL PAPER August 11, 1917

THE POLLINATION OF THE MANGO.

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INTRODUCTION.

In attempting to establish mango culture upon a commercial basis in southern Florida, the Department of Agriculture has introduced during the last 25 years a large number of varieties from India and other important mango-growing regions. In fact, the Tropics have been searched for the best mangos which they produce, and it is probable that the collection now growing in Florida embraces many of the best varieties in cultivation.

The fruiting habits of some of these varieties, however, have not been satisfactory. Several of them fruit very sparsely except in occasional seasons. The Mulgoba, the best variety of all from the standpoint of quality of fruit, has yielded a good crop on an average once in four years. Even at best, some of the varieties seem incapable of producing heavy crops of fruit.

Contrasted with these conditions, most of the common seedling mangos of southern Florida and tropical America are enormously productive and rarely fail to produce a crop.

Numerous explanations have been offered to account for this defect of the choice introduced varieties, but so far as known no investigations have been made with the definite object of determining the precise cause or causes of unfruitfulness and of finding some remedy. A few years ago the trouble was attributed to anthracnose

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(*Colletotrichum gloeosporioides* Penzig), a fungus which frequently attacks the young flower spikes and destroys them. Its activities are largely dependent upon weather conditions, being greatest when the air is warm and moist, with frequent showers. This question was studied by McMurran.[1] Sometimes the flowers appear in dry weather and escape unharmed, but a few days of showery weather later on may provide favorable conditions for the development of the fungus, and the young fruits may be destroyed or badly disfigured and deformed. In some seasons trouble from this source is relatively slight, in others serious.

Allowing for injury from this cause, which is an important factor in the production of mangos, it was believed that there must be other factors responsible for many of the crop failures of the Mulgoba and other varieties. Several Indian and West Indian writers have suggested that defective pollination might be one of the most important factors, and it was for the purpose of determining its precise importance that the investigations herein described were undertaken at Miami, Fla., in 1915 and were continued in 1916. In connection with any studies such as this on the pollination of fruit-bearing trees, two papers by M. B. Waite[2] should be examined.

THE MANGO FLOWER AND ITS POLLINATION.

It has been affirmed by Hartless[3] that the mango is largely, if not solely, wind pollinated. Other writers have also advanced the opinion that the wind is an important agent in effecting pollination.

It seems evident, however, that the mango has none of the characteristics of an anemophilous plant, but, on the other hand, presents well-developed adaptations to insect pollination, so that it may be considered truly entomophilous. The amount of pollen which reaches the stigmas was found to be slightly greater in one instance on a very windy day; but this undoubtedly was due to the brushing of one flower against another or against the surrounding foliage, the panicles being thrashed violently about.

Some of the principal characteristics of an anemophilous plant are that (1) the pollen is abundant, compensating for the enormous waste in transport; (2) the pollen grains are dry and incoherent, so that they are easily carried by the wind; and (3) the stigmas are commonly large and bushy and freely exposed, so as to have every chance of catching the floating pollen grains. The mango has none

[1] McMurran, S. M. The anthracnose of the mango in Florida. U. S. Dept. Agr. Bul. 52, 15 p., 4 fig., 4 pl. 1914.

[2] Waite, M. B. The pollination of pear flowers. U. S. Dept. Agr., Div. Veg. Path. Bul. 5, 110 p., 5 fig., 12 pl. 1894.

——— Pollination of pomaceous fruits. *In* U. S. Dept. Agr. Yearbook, 1898, p. 167–180, fig. 32–44. 1899.

[3] Hartless, A. C. Mango crops and some factors influencing them. *In* Agr. Jour. India, v. 9, pt. 2, p. 141–159. 1914.

of these characteristics; it produces comparatively few pollen grains, often not more than 200 in an anther, and never more than 1,200 in any that were examined; and it must be remembered that this represents the total number produced by one flower, since there is commonly but one fertile stamen. The pollen grains show a decided tendency to cling together, especially in damp weather; and even on bright, sunny days it was found difficult to dislodge them from the anther by subjecting them to the full draft of an electric fan for 30 minutes, most of the grains still clinging to the anther at the end of that time. The stigma is exceedingly small and not provided with projections of any sort to assist in catching pollen.

On the other hand, the production of honey for the attraction of insects shows a distinct adaptation to insect pollination. The structure of the flower is such as to entitle it, apparently, to be placed in Müller's biological class "A", or "flowers with freely exposed honey."[1] Flowers of this class are visited by insects of several orders, from the short-tongued Coleoptera to the long-tongued Lepidoptera, and members of both these orders, as well as of Diptera and Hymenoptera, have been observed on mango flowers, as will be described later on.

STRUCTURE OF THE FLOWER.

The mango is polygamous and produces its flowers on terminal panicles varying in length from a few inches up to 2 feet, each panicle carrying from 200 or 300 up to more than 4,000 flowers, of which only 2 or 3 per cent are perfect in some instances; in others as many as 60 or 75 per cent. (Pl. I.) The character of the panicle and the number of flowers produced upon it vary with different varieties, as also the length of time they remain in bloom. Some varieties remain in flower but 10 days, others for nearly 2 months, and on one panicle of the Sandersha 4,200 flowers were counted which opened at the rate of 20 to 240 a day, extending over a period of 40 days.

The individual flower[2] is subsessile, 6 to 8 millimeters in diameter when the corolla is outspread, the calyx composed of five ovate-lanceolate, finely pubescent, concave sepals and the corolla of five elliptic lanceolate to obovate-lanceolate petals, 3 to 4 millimeters long, whitish, with three or four fleshy orange ridges toward the base, and inserted at the base of a fleshy, almost hemispherical disk, obscurely 5-lobed and usually about 2 millimeters in diameter. In the perfect flower the disk is surmounted by a globose-oblique

[1] Müller, Hermann. Alpenblumen . . . p. 485. Leipzig, 1881.
Knuth, P. E. O. W. Handbook of Flower Pollination . . . v. 1, p. 64. Oxford, 1906.

[2] The structure and development of the mango flower have been briefly discussed by Burns and Prayag. (Burns, W., and Prayag, S. H. Notes on the inflorescence and flowers of the mango tree. *In* Poona Agr. Col. Mag., March, 1911.)

ovary 1 millimeter broad, with a slender lateral style about 2 millimeters high. To one side and inserted upon the disk is the single fertile stamen, composed of a slender subulate filament about 1.5 millimeters long, surmounted by an oval, purplish red anther 0.5 millimeter long, which dehisces longitudinally. (Pl. II.) Occasionally two such stamens are produced. The whorl is completed by staminodes of varying prominence, short and subulate in some varieties, larger and capitate in others, some even becoming fertile and producing a few pollen grains. In the staminate flower the ovary is wanting.

ANTHESIS AND LIFE OF THE FLOWER.

Anthesis may take place at any time of the day or night, but it seems to be most frequent early in the morning. Usually a large number of buds will be seen to be opening about 6 or 7 o'clock and if the weather is clear the petals will be fully expanded and the anthers dehisced by noon. On exceptionally warm, bright days the anthers sometimes dehisce before the petals are fully expanded. Other flowers may open later in the day, and a few during the night.

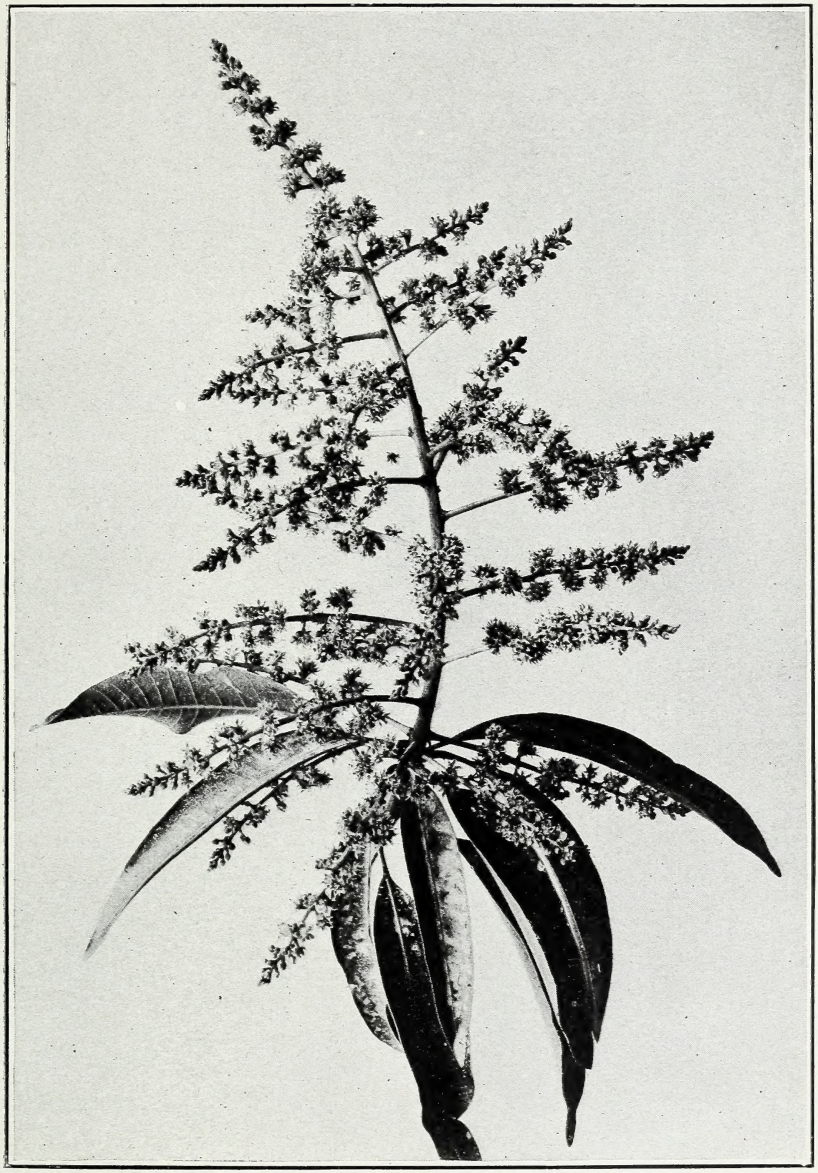
The stigma has every appearance of being in a receptive condition immediately after anthesis, and in favorable weather retains its fresh appearance for about two days. At the end of this time the pistil usually commences to turn brown toward the stigmatic end, and the ovary may commence to swell and assume a darker green color. In many flowers, however, the ovary swells but little, the flower drying up and falling off on the third or fourth day.

In flowers which have opened before noon, the pollen usually remains clinging to the anther for several hours, gradually being brushed off by insects or eventually falling. Sometimes much pollen will be left upon the anther until the second day. If the flower is staminate, usually it will shrivel and fall by the third day. Conditions seem to be vastly more favorable for pollination immediately after anthesis than at any later time, because of the larger amount of pollen present. No indications of heteracmy were observed, the stigma appearing to be receptive as soon as the flower opens, usually not more than an hour or two before the anther dehisces. It remains receptive for some time.

POLLINATION.

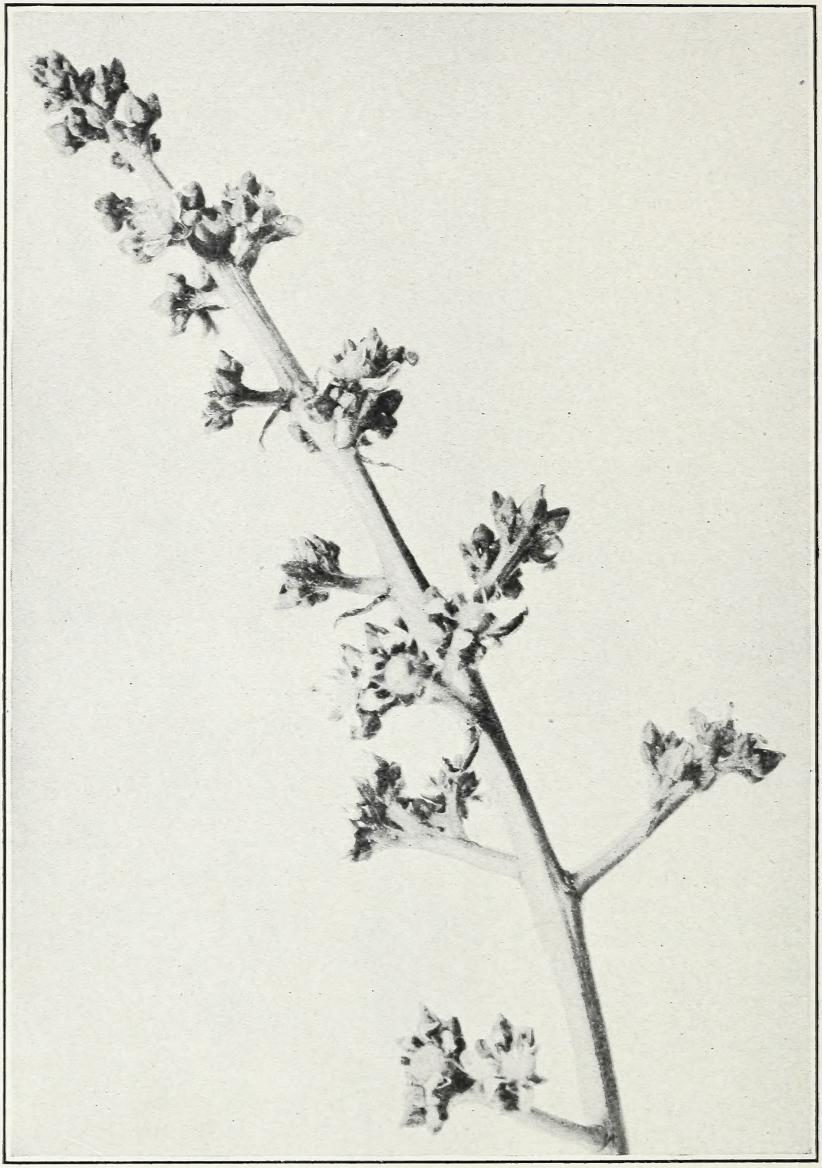
In spite of the close proximity of anther and stigma, the transfer of pollen from the former to the latter does not seem to be accomplished easily. Both the stamen and the pistil retain an erect position throughout, and the pollen as it is shed usually falls upon the base of the ovary or upon the disk rather than upon the stigma.

The normal method of transferring the pollen from the anther to the stigma must be through the agency of insects. The white,



INFLORESCENCE OF THE BRINDABANI MANGO.

This Indian variety produces larger panicles than many others, the length of the one here shown being about 14 inches. (Photographed by Wilson Popenoe at Miami, Fla., April 7, 1916; P16706FS.)



FLOWERS OF THE WHITE ALFONSO MANGO. SLIGHTLY ENLARGED.

Apex of a panicle, showing the character of the individual flowers, some which show the ovary, style, and stamen indistinctly. In this variety the perfect flowers are the first to open (at least toward the apex of the panicle), and are followed later by many staminate ones. (Photographed by Wilson Popenoe at Miami, Fla., April 7, 1916; P16703FS.)

tumid disk secretes a thick, sweetish fluid which stands out upon its surface in small globules, collecting in larger quantities at the bases of the petals. Insects are attracted to this nectar by the fragrance of the flowers, presumably, and their visits are numerous, especially during the early hours of the day, from daylight until 9 or 10 o'clock a. m. Many insects were observed feeding upon this nectar, and after their visits it was found that there was practically none of it left upon the disk. In moving over the flower in order to get at all sides of the disk, it is almost impossible for an insect of any considerable size to avoid brushing against the anther and dislodging some of the pollen, and in this way transferring the pollen to the stigma, since it is sufficiently rough to cling to the body of the insect and its transport can be effected. It is evident, however, from the comparatively small number of stigmas pollinated that large quantities of pollen are not carried on the bodies of insects, and this belief was confirmed by observation. Examination of insects taken from the flowers has never revealed more than seven or eight pollen grains clinging to their bodies, and not more than one to three or four grains were usually found. The pollen itself is not very abundant, and the number of grains which become attached to the body of each insect visitor is certainly not large.

Of the principal insects observed upon the flowers of the mango in the vicinity of Miami it is necessary to treat in some detail. Those which were captured during the months of March, April, and May, 1915, when most of the mangos were in bloom, and have been identified by the Bureau of Entomology, through the courtesy of Dr. L. O. Howard, Chief, represent the four orders Diptera, Hymenoptera, Lepidoptera, and Coleoptera, ranking about in the order given as to the importance and frequency of their visits. The flies are the only insects which are nearly always present upon mango flowers at any time of day. As they are not so active as some of the Hymenoptera and remain upon a single flower for a longer time, they are scarcely so conspicuous in the early morning as some of the latter, which on sunny mornings can be seen buzzing about the trees in considerable numbers. The commonest fly which was taken on mango flowers was *Ravinia* sp., an insect slightly larger than the common house fly, with a grayish body. Somewhat less common were two species of Sarcophaga, with bodies about 1 centimeter in length, the thorax longitudinally striped with black but the general color grayish. A bluebottle fly (*Lucilia caesar* L.) and another bluish green species slightly larger than a house fly, the screw-worm fly (*Cochliomyia macellaria* Fab.), were not common, but a few specimens were taken. Still less common were two very large flies, one a horsefly (*Tabanus americanus* Forst.) which was seen upon the flowers occasionally, and another (*Volucella esuriens* Fab. var.

mexicana Macq.) a bluish black species with a very broad body about 1.3 centimeters long, which was seen only once or twice.

Among the Hymenoptera one of the most important was the honeybee (*Apis mellifera* L.); yet this insect did not appear to visit the mango with much regularity, being found in considerable numbers at certain times but scarcely coming near the trees on other days, and only observed in certain sections, presumably where apiaries were near by. Perhaps the irregularity of its visits may be due to the fact that it does not find much honey on the mango flower and visits it only when there is a scarcity of other material. The industry with which the honeybee goes from flower to flower, systematically working over the surface of the disk with its proboscis to obtain all the nectar present, at the same time turning its body around in a circle and almost of necessity coming in contact with the anther in its circuit of the disk, makes this insect one of the most effective pollinating agents.

Two other Hymenoptera which visit the mango with great frequency are *Stenodynerus* sp. and *Stenancistrocerus bifurcus* Rob., small wasps with rather slender dark-brown bodies, which in most sections were found more commonly than the honeybee. *Gorytes* sp. is another small wasp somewhat similar in appearance to the last and about as common; *Cerceris* sp. is smaller and was found much less commonly. A somewhat larger wasp, with a particularly prominent head, *Hypocrabro 10-maculatus* Say, and a smaller and lighter colored one, *Tachytes* sp., are two others which were occasionally found. Of the larger wasps, several visited the mango with great frequency, especially during the early morning hours, but it is doubtful whether they are as effective in transferring pollen as the honeybee, the smaller wasps mentioned above, and flies, since their long legs usually keep their bodies at some distance from the essential organs of the flower. A small species, *Arachnophroctonus* sp., is probably the most common one observed and was seen with great regularity, though not in such numbers as several of the smaller wasps. *Palmodes abdominalis* Cress., *Chalybion coeruleum* L., *Polistes crinitus* Fab. var., *P. rubiginosus* Lep., and *Sceliphron cementarium* Dury are others which were taken, but these probably did not have a great deal to do with pollination.

The sole lepidopteran which was collected on mango flowers was the coontie butterfly (*Eumaeus atala* Poey), a species very common in southern Florida and one for which the mango seems to possess considerable attraction. Several dozen specimens were noted on a single tree at one time, and some of them were seen taking up the nectar from the disk with their long probosces. Several of these butterflies were examined to see if pollen could be found clinging to their

bodies, and although a few grains were nearly always present no considerable quantities were ever seen.

While four beetles were taken on mango flowers, one of them with considerable regularity, it is doubtful whether any of the Coleoptera plays an important part in pollination. The common species was *Euphoria sepulcralis* Fab., a grayish black, clumsy insect with a broad body about 1 centimeter long. *Chauliognathus marginatus* Fab., a slender, much smaller, and more active insect, was seen in one locality on several different occasions. *Pachnaeus opalus* Oliv., a pale-green species slightly under 1 centimeter in length, was taken only once, as was also *Chrysobothris chrysoela* Ill., a small black species with six shining red spots on the wing cases. It is doubtful whether either of these has a bearing on pollination.

In spite of the visits of the above-mentioned insects, a large proportion of the stigmas are unpollinated, and it seems probable that very little pollen is transferred from one flower to another, most of the stigmas probably receiving pollen from the anther of the same flower. Examinations were made of numerous flowers to determine the number of pollen grains which had lodged on the stigma. For this purpose those flowers were chosen in which all, or practically all, of the pollen had been shed from the anther, but in which the stigma had not yet commenced to turn brown. Such flowers had every opportunity to be pollinated and where they were found to be unpollinated at that time there was very little chance of their being pollinated at all, since the stigma would have soon been past the receptive stage. An examination of 429 such flowers gave the following results:

	Number.		Number.
Stigmas unpollinated	223	On which 4 grains were found	26
On which 1 grain was found	84	On which 5 grains were found	13
On which 2 grains were found	47	On which 6 grains were found	5
On which 3 grains were found	26	On which 7 to 10 grains were found	5

The flowers examined were taken from trees in different sections around Miami and under widely differing weather conditions, so that the results probably can be considered a fair average of normal pollination for this region. Differences were noted in the comparative abundance of pollination on different days and different trees, of course, but with one exception these seemed scarcely important enough to warrant notice. After a rather strong wind which blew for about two days, a higher per cent of pollination was found on the Sandersha variety than at any other time. Coupled with this was the presence of large quantities of foreign matter on the pistils, principally fine particles of sand. The flowers had been thrashed about considerably in the wind, and more pollen had reached the stigmas than was normally found in calm weather.

In damp, cloudy weather the pollen grains swell and are much more difficult to dislodge than when the weather is dry and sunny.

After a heavy dew they will be found in this swollen condition, but if not washed off the anther they will be found later in the day, if the sun has come out, to have resumed their normal dry form, oblong-oval.

THE PISTIL.

It has been suggested that some of the unproductive varieties might be found to have abortive pistils and hence to be incapable of being properly fertilized. For this reason the pistils of every available variety were examined. The only difference noticeable among most of them was a slight variation in the width or expansion of the stigma; in some varieties the stigma is not expanded at all, being no wider than the style below it; in a few others it is commonly slightly expanded, and flattened on the upper surface. A V-shaped cleft is frequently visible in the outer edge of the stigma, extending downward in the form of a gradually narrowing groove and finally disappearing. In the freshly opened flower the pistil stands nearly erect, but the stigmatic surface is often slightly to one side and facing away from the center of the flower. Frequently the upper end of the style is curved slightly in this direction, especially when the flower commences to get old.

On one tree only were the pistils found to be commonly abortive; this was a Mulgoba seedling on the Hugh Matheson place at Cocoanut Grove. On this tree many of the pistils were exceedingly short or almost entirely aborted, the rudiments of the style persisting in the form of a short point on the upper surface of the ovary. Some of the pistils seemed to be normal, but a great many were in this abortive state and certainly incapable of being fertilized.

PROTECTION OF POLLEN FROM DEWS AND RAINS.

A frame was erected over one side of a young tree of the Julie variety and a canvas curtain placed over it every afternoon about 4.30 o'clock and removed in the morning soon after sunrise. This curtain was also put over the tree whenever a shower threatened. One-half of the tree was left exposed to the elements as a check. It was thought that by protecting the flowers from rain, so the pollen would not be washed away, there might be a better chance of pollination. By carefully comparing the flowers on the covered and uncovered sides of the tree on days when the weather was fair or showery or there had been a heavy dew the previous night, it became evident that the protection afforded could not be of much practical benefit. The covering did not prevent the access of sufficient moisture to cause the pollen grains to swell and become sticky, and although it prevented the pollen from being entirely washed away by a shower it did not seem to have a great deal of bearing upon the average of pollination. The cover was kept on for several weeks and then

removed entirely. There was no appreciable difference between the covered and the uncovered sides of the tree in the number of fruits produced.

THE POLLEN.

SHAPE AND CHARACTERISTICS OF THE POLLEN GRAIN.

In its normal dry state the pollen of all varieties examined exhibited an oblong-oval form, slightly broader in some varieties and narrower in others, but approximating the same shape in all. When moistened by being placed in water the grains immediately swell and in a very few seconds have become spherical in outline, but on being allowed to dry out they resume their oblong-oval form. Under the microscope the dry pollen grains exhibit one or two sutures extending longitudinally; these disappear when the grain is moistened and swells. The thick outer membrane, or extine, is rugose on the surface and contains four pores, through one of which germination takes place. These pores frequently show very plainly after the pollen grains have been in a culture medium for 24 hours, the intine often protruding slightly from each of them. There are slight differences in the form of the ungerminated pollen grains of different varieties after they have been left for several hours in the culture medium; thus, it was noted that in some varieties the ungerminated grains commonly assumed a distinctly triangular outline, those of another variety were almost spherical, while those of still another were slightly oblate in form.

NUMBER OF POLLEN GRAINS PRODUCED BY THE ANTHERS.

The greatest variation was found in the number of pollen grains produced by the anthers, not only among different varieties but in different anthers from the same tree. The smallest number was found in the anthers of the No. 11 seedlings examined at the Royal Palm Nurseries, Oneco, Fla. The trees were just coming into bloom after rather cold weather, and the flowers did not appear to be strong. The anthers were in many cases rather weakly developed and contained only 35 to 100 pollen grains, 200 being the largest number counted. Later in the season more than 400 grains were counted in anthers from other trees of this same race. The highest number counted was about 1,200, in the anthers of the Mullgoa (not Mulgoba), a variety in which staminate flowers greatly predominate and which produces more pollen than many others. An average number of pollen grains probably could be established for each variety and would be found to vary considerably in different varieties, some averaging not more than 400 or 500, while others certainly would go as high as 700 or 800.

PROPORTION OF PERFECT AND ABORTIVE POLLEN GRAINS.

On examination of the pollen of one variety in January it was found that some of the pollen grains were either small or appeared to be empty. Following up this observation, an attempt was made to determine whether the proportion of poor grains was larger in unproductive varieties than in productive ones and whether this question might have any bearing on the productiveness of a variety.

Early in the season a much larger proportion of poor pollen was found than later on, when the weather was warm and the flowering normal. At the latter time no variety was found in which the number of defective pollen grains would average over 8 or 10 per cent at the highest, and usually it did not average more than 2 to 4 per cent of the total. The number varied greatly in different anthers of the same variety; thus, in the Bennett as much as 25 per cent of empty grains was found in one anther, but this was exceptional and the number of poor grains normally found in this variety was insignificant.

Defective pollen grains are of two kinds: (1) Those which are undersized and (2) those which are empty and appear as irregular, collapsed bodies of a darker color when seen under the microscope. Frequently there is considerable variation in the size of the pollen grains, many being somewhat smaller than normal and a few being very small. The average of every variety, however, shows a very small proportion of grains which are abnormal in appearance, the vast majority being uniform in size and shape, plump, and apparently perfect.

ARTIFICIAL CULTURE OF THE POLLEN GRAINS.

The method used in the artificial culture of the pollen grains was that of Max Pfundt.[1] On a glass slide a small glass ring was mounted; a drop of the culture medium was then placed on a cover glass and this inverted over the ring, the edge of which had been previously greased with vaseline to exclude the air. The bottom of the chamber inclosed by the glass ring was covered with the culture solution in order to keep the vapor tension within the chamber as uniform as possible and to avoid the slightest change in the concentration of the hanging drop. Pollen was sown upon this hanging drop, previous to placing it over the glass ring, by taking a stamen upon which pollen was freely exposed, holding it in the forceps, and lightly touching the surface of the drop in several places. The culture thus prepared was labeled and between observations placed in a large glass moist chamber. Following the method of Pfundt, this moist chamber was kept in the dark.

A considerable amount of experimentation was necessary before a successful culture medium was obtained. Cane-sugar solutions

[1] Pfundt, Max. Der Einfluss der Luftfeuchtigkeit auf die Lebensdauer des Blütenstaubes. *In* Jahrb. Wiss. Bot., Bd. 47, Heft 1, p. 6–33. 1909.

of densities varying from 1 to 75 per cent were tried, gelatine or leached agar-agar being added to them in varying amounts. Finally, it was found that the best results were obtained with a sugar solution of 25 per cent to which 0.5 per cent of agar-agar had been added. To make this, a 50 per cent solution of cane sugar was prepared and sterilized and then to 10 c. c. of this solution an equal amount of 1 per cent leached agar-agar[1] was added. The sugar solution was made up by weight, one-half ounce of cane sugar being added to 1 ounce of distilled water. Before using the culture medium it was sterilized and after two or three days resterilized, repeating this process two or three times, after which a new solution had to be prepared.

In solutions of a density less than 20 per cent many of the pollen grains burst within a few minutes, as they do in water, and in solutions of a greater density than 30 per cent no germination took place.

The effect of temperature upon the germination of the pollen appeared to be of the greatest importance, and many failures during the early part of the work, when the nights were cold, can probably be attributed to this cause.[2] Later in the season a few experiments were made to determine the minimum temperature at which germination would take place. Cultures were made as usual, six of one variety, and three of them placed in the ice box, the other three in the moist chamber at room temperature as a check. The result was that no germination took place at 55° F.; at 60° F. there appeared to be a feeble germination of a few grains; at 65° F. the germination was a little better, but still below normal. The best results were obtained between 75° and 80° F., nearer 80° than 75°. No cultures were tried in a temperature above 80° F., which was the highest reached in the moist chamber kept in the laboratory. It seems doubtful whether mango pollen can be expected to germinate normally at a temperature below 60° F.

As to the time required for germination, numerous cultures were examined at the end of 30 minutes, 1 hour, 2 hours, and so on, with the result that at a temperature of 76° F. the first signs of germination were visible within 1 hour. At the end of this time the tubes had not yet reached a length equal to the diameter of the pollen grain, but at the end of 2 hours and 15 minutes the longest pollen tubes were in length almost twice the diameter of the pollen grain. In order to give the pollen tubes time to develop to as great a length as possible, most of the cultures were allowed to remain 12 to 24 hours before examination; at the end of this time development seemed to

[1] This material was obtained from Dr. Albert Mann.

[2] The failure of McMurran to germinate mango pollen (McMurran, S. M., The anthracnose of the mango in Florida, U. S. Dept. Agr. Bul. 52, 15 p., 4 fig., 4 pl., 1914) may have been due to cold weather at the time the attempt was made.

have ceased, as no further changes were produced by leaving the cultures longer. (Fig. 1.)

RESULTS OF GERMINATION TESTS.

By the method described, cultures were made of pollen from all the varieties which it was possible to obtain near Miami, including

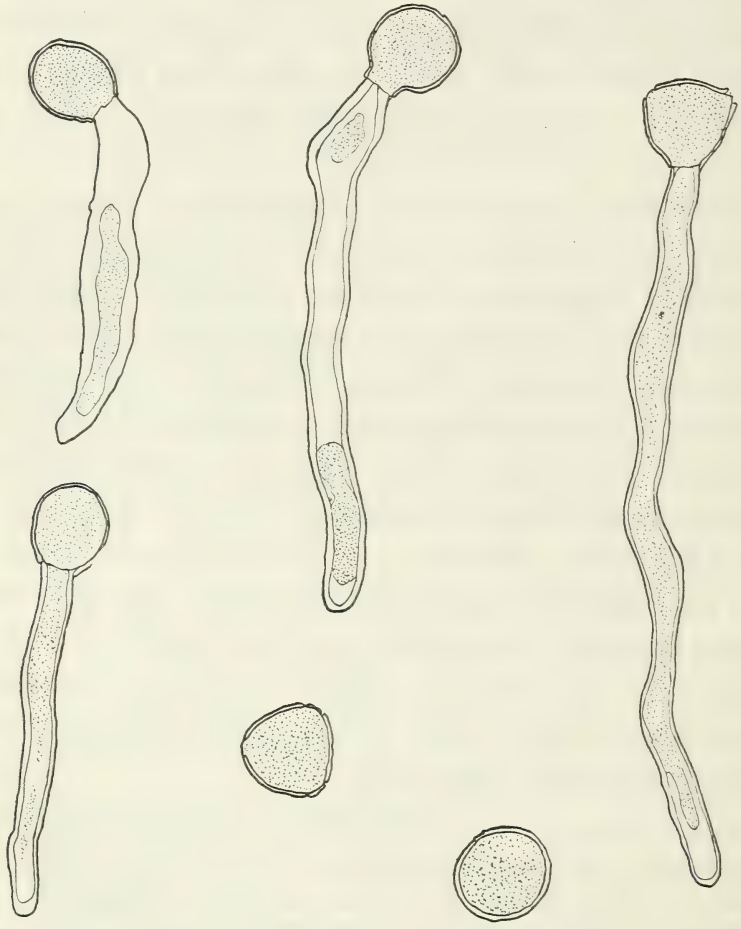


FIG. 1.—Pollen grains of seedling mango of No. 11 type after 24 hours in a 25 per cent sugar solution, showing the development of the tubes. Greatly magnified.

several seedlings. The percentage of germination was in no case high and did not indicate that the superior productiveness of some varieties was due to the greater viability of the pollen. It was significant, in fact, that the best germination was obtained with a variety which is markedly unproductive, the Mullgoa. In the seedling No. 11 race, also, a comparatively good germination was obtained in several instances, while the Mulgoba variety was one of the most

difficult of all to germinate. The percentage of grains which sent out pollen tubes varied from 0 to a little more than 50, but in the vast majority of the cultures would not average above 10 or 15 per cent. No pollen tubes developed to a length exceeding seven times the diameter of the pollen grain, and commonly they did not exceed four or five diameters. Without going into detail regarding the cultures, of which about 300 were made, it can be said that the germination of all varieties was very poor. While the percentage of germination was higher in some varieties than in others, it varied in the same variety upon different days, though the conditions were as nearly similar with regard to culture medium and temperature as it was possible to keep them. The percentage of germination and the vigor of the pollen tubes were greatly inferior to those obtained in cultures of the feijoa (*Feijoa sellowiana*), the lumbang (*Aleurites moluccana*), or several other plants which were tested. It has been pointed out by Prof. E. J. Kraus, however, that pollen germinations made under moist-chamber conditions do not necessarily indicate the germinability of the grains on the stigmas under optimum conditions.

THE PRODUCTION OF FRUIT.

The stigmas, as has been shown, receive no pollen in more than half the instances; and of those cases where they are pollinated, in comparatively few are there more than one or two grains upon each stigma.

Under these conditions it was thought that the production of fruit might be increased noticeably if the stigmas were pollinated more abundantly; with ample pollination, even if some of the pollen grains were defective, a few capable of developing pollen tubes and reaching the ovum should reach each stigma. Working on this theory, a number of hand pollinations were made.

On a 6-year-old tree of the Bennett variety at the E. B. Douglas place, Buena Vista, Fla., five panicles of flowers were selected for hand pollination, and on two days, April 28 and May 1, 1915, pollen from the same tree was applied to all the fresh stigmas on each panicle. The exact number pollinated on each panicle was as follows:

Panicle No. 1.....30 stigmas.
Panicle No. 2.....25 stigmas.
Panicle No. 3.....31 stigmas.
Panicle No. 4.....25 stigmas.
Panicle No. 5.....51 stigmas.

These were not all of the perfect flowers on each panicle, but it was thought advisable to pollinate only those stigmas which appeared to be fresh and in a receptive condition at the time the work was done. No fruits were carried on any of these panicles, though on May 21 about 60 well-formed fruits were counted on other panicles

throughout the tree. There were many panicles throughout the tree on which there were no fruits, aside from those which were hand-pollinated.

Other hand pollinations (all with pollen from the same tree) were made in 1915, as follows:

Mullgoa.—Panicle No. 1, all fresh stigmas, pollinated on six successive days. Panicle No. 2, all fresh stigmas, pollinated on five successive days. No fruits were carried on either one, although there were a few fruits on other parts of the tree.

Malda.—One panicle, on which all fresh stigmas were pollinated on five successive days, 243 stigmas in all. No fruits set, and there were only two elsewhere on the tree.

Kala Alfonso.—All fresh stigmas on one panicle, hand-pollinated on two successive days. No fruits set, and none elsewhere on the tree. Perhaps the tree was too young; this was its first year of flowering.

White Alfonso.—One panicle, all fresh stigmas, hand-pollinated on three successive days. Set well, agreeing with the other panicles on the tree.

Amini.—One panicle, all fresh stigmas, hand-pollinated on four successive days. One fruit carried, agreeing with several other panicles naturally pollinated.

Sandersha.—Two panicles hand-pollinated on several successive days. Set several fruits but carried none; behavior differed in no way from many others naturally pollinated.

In general, it may be said that the quantity of fruit produced in all the above cases agreed with the average of other panicles on the tree which were not hand-pollinated. In other words, no appreciable effect was produced by applying an abundance of pollen to the stigmas.

In 1916 this experiment was repeated on a small scale, and in addition an attempt was made to determine whether or not cross-pollination would increase the production of fruit; and an experiment was carried on to determine whether fruits would be produced without the pollination of the stigmas. This latter experiment was suggested by the investigations of Belling [1] who studied young ovaries of the polyembryonic No. 11 race and found that all the embryos appeared to be adventive, no trace being seen of the fertilized egg cell and no traces of pollen tubes being found in the styles. This suggested that fertilization might not be necessary for the development of these polyembryonic mangos.

In order to manipulate the flowers more readily and lessen the danger of contamination, all the lower laterals were removed from the panicles operated upon in 1916, leaving only the flowers upon the upper 4 or 5 inches of the panicle. Working with the whole panicle, which may produce 4,000 flowers, it is next to impossible to insure that no anthers are allowed to dehisce or that some of the stigmas are not accidentally pollinated. The panicles were all inclosed in fine muslin bags stretched over a wire frame attached to the branch below the base of the panicle.

[1] Belling, John. Report of assistant in horticulture. Mango. *In* Fla. Agr. Exp. Sta. Rpt. [1907]/08, p. cx-cxxv, pl. 7-10. [1908.]

A large seedling tree of the No. 11 race, growing on the property of Prof. P. H. Rolfs, at Buena Vista, near Miami, was selected for the principal experiments. On this tree two panicles were bagged, preventing the access of insects, and left to determine whether any fruits would develop without the agency of insects in effecting pollination. The result was that no fruit developed. While the experiment was on a very limited scale, the No. 11 race is exceedingly productive and usually carries a large number of fruits on each panicle, so that a failure to carry any fruits is much more significant than it would be in such a variety as the Mulgoba. This experiment was conducted on several other trees, with the same result in every case.

Two panicles on the same tree were bagged before any of the buds had commenced to open (as in the others), and as rapidly as the flowers appeared the stamens were removed before they had commenced to dehisce. Emasculation was continued until the last flower had opened, and the bags were then left on until ample time had elapsed for the fruits to develop; but all dropped off, indicating that pollination is necessary, even though the egg cell may not develop into an embryo, as appears to be the case from Belling's investigations. This experiment was tried in about 10 other instances, with the same result in each. In a few cases fruits developed parthenocarpically to the length of about 1 inch and then dropped.

Two more panicles on this tree were bagged for hand pollination, and as rapidly as the flowers opened the stigmas were pollinated with pollen from flowers on the same tree. On one panicle 36 stigmas were thus treated, and on the other 30 stigmas. The first panicle carried seven fruits and the second two. This is somewhat more than the average of other panicles on the tree, considering the fact that only a small portion of the panicle was allowed to develop, all the laterals having been removed.

Two more panicles were bagged for cross-pollination and the flowers emasculated as soon as they opened, so that no pollen was liberated within the bag. Pollen of the Sandersha variety from a near-by tree was applied to all fresh stigmas once each day, a total of 83 being pollinated in the first instance and 66 in the second. Seven fruits were carried by the first panicle and six by the second, a considerably larger number than is usually produced by an equal number of flowers on a panicle left to be pollinated naturally. Probably all of these fruits would not be carried to maturity. When last examined, they were one-half to 1 inch long.

Cross-pollination gave equally good results with other varieties. It was tried on the Madras variety, with the result that 8 fruits developed from 58 pollinations, the pollen being taken from a tree of the Cambodiana mango. The Alfonso, when pollinated by this

same variety, set 6 fruits from 47 pollinations. The Sandersha, pollinated by the same variety, set 10 fruits from 52 pollinations. The Paheri, pollinated by the same variety, set 2 fruits from 59 pollinations. Pollinated by the Sandersha, the Paheri set 17 fruits from 92 pollinations.

Though the best results were obtained from cross-pollination, nothing has been found to indicate that any of the varieties are self-sterile. Both the experiments in self-fertilization and the behavior of many isolated mango trees in southern Florida and elsewhere indicate that the mango is normally self-fertile.

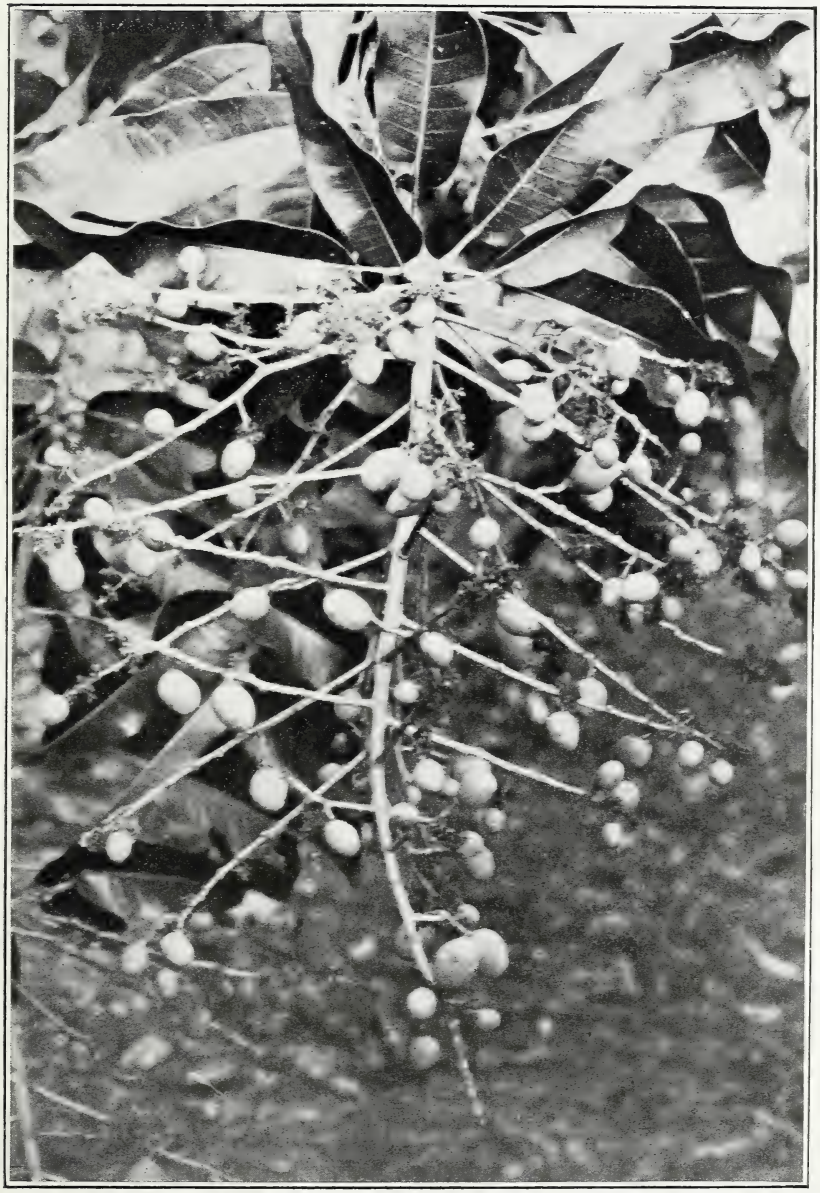
From the fact that pollination ordinarily is scanty, it might be concluded that productiveness could be increased by insuring more abundant pollination. While this is perhaps true, a careful consideration shows this point to be of comparatively little practical importance. The total number of flowers produced is so enormous that it is usually of small consequence if half of the perfect ones fail altogether to receive pollen (Pls. III and IV). In practically all of the seedling mangos it has been observed that the trees often set many more fruits than they can carry to maturity, and this has been noted with the Bennett, Cambodiana, Haden, and other budded varieties as well. Possibly it might be of importance in the case of varieties producing a very small number of perfect flowers, such as the Mullgoa and the Jamshedi, but in the varieties which are being planted commercially in Florida the percentage of perfect flowers is satisfactorily large.

FLOWERING HABITS OF THE MANGO.

Different races and varieties of the mango exhibit well-defined characteristics of flowering, both with regard to flowering under adverse climatic conditions and with regard to the abundance of flowers produced and the length of time the tree remains in bloom. There are also marked differences in the proportion of perfect to staminate flowers in different varieties and in the distribution of the perfect flowers upon the panicle.

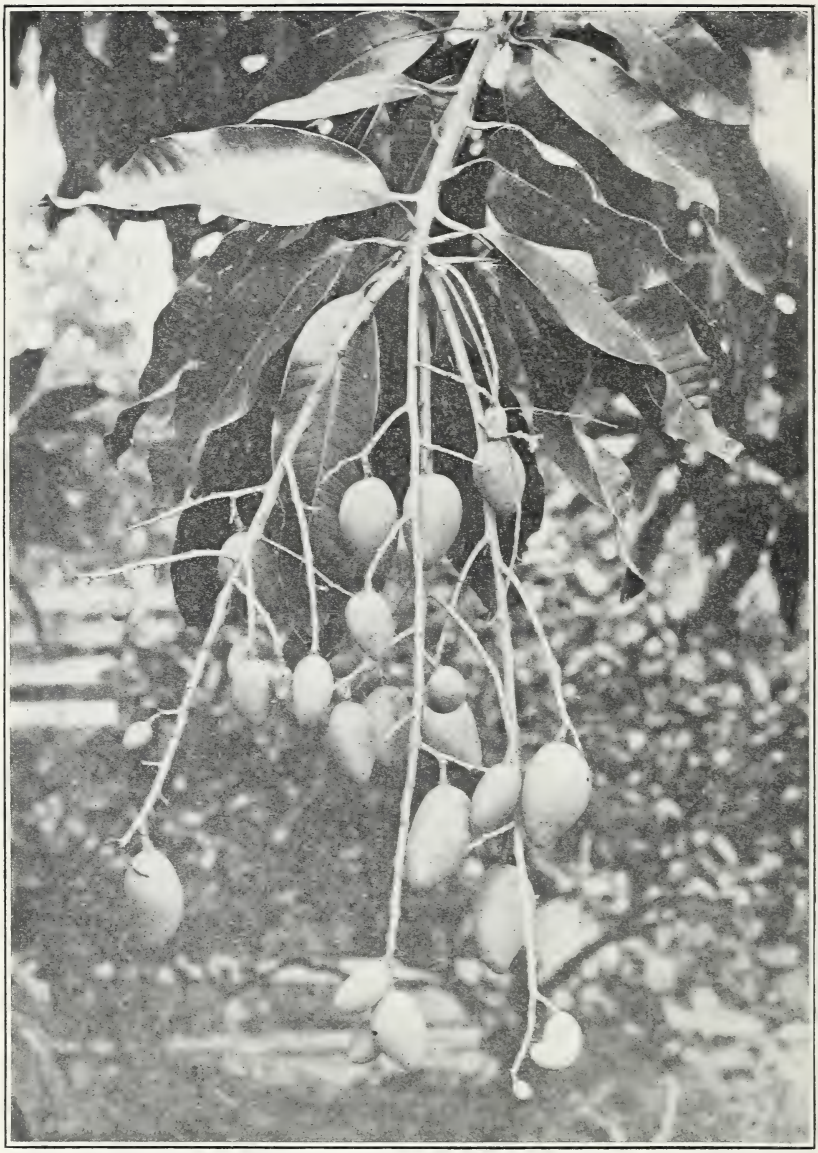
REGULARITY OF FLOWERING.

There can be no doubt that the production of flowers is strongly influenced by the soil moisture during the normal blooming season. This fact has not only been noted by various observers in Florida, but has been recorded elsewhere. In some sections where the ground is low and continually moist, the mango rarely flowers, while in regions where there is a well-defined dry season corresponding to the normal flowering season, allowing the soil to dry out thoroughly, flowers are produced abundantly. From the behavior of the numerous varieties and seedlings in the vicinity of Miami, it is apparent



YOUNG FRUITS ON ONE PANICLE OF A PHILIPPINE SEEDLING MANGO.

The seedling race of mangos known as the Philippine, or Filipino, is grown in Cuba and Florida and sometimes produces heavy crops, with many fruits to the panicle. The panicle here shown was pollinated naturally and shows the profusion of fruits which often develop. Many of these will drop, not more than four or five usually being matured. (Photograph taken by Wilson Popenoe at Herradura, Cuba, February 20, 1916; P16665FS.)



PARTLY GROWN FRUITS ON A SEEDLING MANGO OF THE PHILIPPINE RACE.

A later stage than that shown in Plate III, many of the young fruits having dropped. The process of thinning will be carried farther, probably not more than four or five fruits eventually maturing on this panicle. (Photographed by Wilson Popenoe at Herradura, Cuba, February 20, 1916; P16666FS.)

that some are affected less injuriously by a wet soil than others. Most notable among those which flower under conditions somewhat unfavorable may be mentioned the Sandersha and the Julie of the grafted varieties and the No. 11 race among the seedlings. During the early spring of 1915, when the weather was unusually wet and the ground was scarcely allowed to dry out, all these came into bloom, while the Mulgoba and numerous other varieties failed to show any signs of bloom until the rains had ceased for a time and the wet spell had been followed by two weeks of dry, sunny weather. It is evident that in many varieties some check to vegetative growth, such as is given by a thorough drying of the soil, is necessary to encourage flowering. While conclusive evidence is lacking, it seems probable that fruit buds are not formed in the mango a long time in advance of the flowering season. This is in contrast to many temperate fruits, such as the apple, in which the fruit buds are formed during the summer, lie dormant over winter, and appear as flowers in the spring. In the mango no indication of tissue differentiation to form fruit buds has been observed in the vegetative cones of the young branchlets until a very few weeks previous to the appearance externally of the young panicle. Thorough drying of the soil a few weeks before the normal flowering season, therefore, should be efficacious in encouraging the formation of fruit buds, and in practice this has proved many times to be the case.

The necessary check to growth sometimes is produced artificially in the Tropics by root pruning, hacking the trunk, or other means. It seems highly desirable, however, that the check be produced normally through the drying of the soil, and hence the best mango regions probably will remain those where the normal flowering season occurs at a time of year when the weather is usually dry. It is significant, however, that some varieties seem to require this check to a less degree than others, and this may make possible the cultivation of choice varieties which will be much more regular in fruiting than the Mulgoba when grown under slightly adverse conditions.

LENGTH OF FLOWERING PERIOD.

In addition to flowering regularly, even when climatic conditions are somewhat unfavorable, another characteristic is important in connection with flowering, i. e., the length of time during which a tree remains in bloom. This varies greatly in different varieties. Some will develop all their flowers within 10 days from the opening of the first buds; other varieties, such as the Sandersha and the Julie, keep on developing new panicles of flowers throughout several weeks, or even months, and in 1915 there was not a single day between the middle of January and the latter part of May on which flowers could

not be found on the Sandersha tree in the Plant Introduction Garden at Miami. This characteristic is of importance, in that it gives the tree a greater opportunity to set fruit; often the attacks of the anthracnose fungus are most severe when a tree is in bloom, and the entire crop of flowers is destroyed. In some varieties this means a crop failure, since the tree will not produce any more flowers during the season; but in the Sandersha (if early in the season) it would merely mean that the flowers which happened to be present at the time the fungus attack occurred would be lost and the flowers which appeared later might happen to strike more favorable weather, when the ravages of the fungus were less severe, and a crop of fruit result. Many of the seedling races possess the ability to flower a second time if one crop is destroyed by fungi. In fact, H. A. Van Hermann states that he has seen seedlings in Cuba flower four times during the winter and early spring months before they succeeded in setting a crop of fruit. The first three crops of flowers, coming at a time when the weather encouraged the growth of fungi, were lost and the tree was forced to bloom again. In case the first crop of flowers results in a good setting of fruit there is no further production of flowers during the season, according to Van Hermann.

PROFUSION OF BLOOM.

Sometimes the entire tree comes into bloom at one time, covering itself with flowers; again, one side of the tree may flower, while the rest of the tree shows no buds, or the flowering may be confined to a small section of the tree, which probably represents the branchlets arising from one main limb. This corresponds to the habit of growth exhibited by the mango, which is noted but not explained by Schimper.[1] Frequently the young branchlets over a small portion of the tree will come in flush while the rest of the tree is dormant. It was noticed during the season of 1915 that a number of Mulgoba trees produced flowers over only a small proportion of their surfaces. It might be expected that the remainder of the tree would flower at another time, but this is by no means always the case.

PROPORTION OF PERFECT TO STAMINATE FLOWERS.

It is true that some varieties which bear heavy crops are characterized by a large percentage of perfect flowers, while others which are known to be unusually regular in fruiting, although they may not produce such heavy crops, are characterized by a rather low percentage of perfect flowers.

The Philippine race, which sometimes produces enormous crops, with several fruits in each cluster, often has more perfect than staminate flowers. The No. 11 race, which also produces heavy

[1] Schimper, A. F. W. Plant Geography upon a Physiological Basis . . . 839 p. Oxford, 1903.

crops, with several fruits arising from a panicle, has a high percentage of perfect flowers. Most of the Indian varieties, which commonly mature but one fruit from a panicle of flowers, usually have a lower percentage of perfect flowers than either the No. 11 or the Philippine race of seedlings. The Haden, however, has a large percentage of perfect flowers and retains the bearing habit of the Indian varieties, though occasionally it matures more than one fruit on a panicle. The Julie, which has a very high percentage of perfect flowers, commonly matures but one fruit on a panicle. It seems very doubtful whether there is any correlation between the percentage of perfect flowers and productiveness.

In some varieties, at least, the perfect flowers do not open continuously during the time the panicle is in flower, but most of them appear within a limited period of time. This is illustrated by a count made of one panicle of Sandersha flowers, showing the number of perfect and staminate flowers which opened each day. (Table I.)

TABLE I.—*Count of one panicle of flowers of the Sandersha mango, showing period of opening.*

Date.	Time of day.	Flowers.			Date.	Time of day.	Flowers.		
		Perfect.	Staminate.	Total.			Perfect.	Staminate.	Total.
March:					April:				
30	4.00 p. m.	0	19	19	16	1.00 p. m.	2	142	144
31	3.30 p. m.	0	21	21	17	10.30 a. m.	1	105	106
April:					18	11.00 a. m.	1	119	120
1	3.15 p. m.	0	38	38	19	2.00 p. m.	0	127	127
3	7.00 a. m.	0	70	70	20	1.00 p. m.	0	132	132
4	1.30 p. m.	0	40	40	21	1.00 p. m.	2	106	108
5	2.30 p. m.	0	37	37	22	2.00 p. m.	2	95	97
6	3.15 p. m.	0	90	90	23	1.00 p. m.	3	100	103
7	1.00 p. m.	0	92	92	25	8.30 a. m.	151	115	266
8	1.30 p. m.	0	104	104	27	10.00 a. m.	152	96	248
9	12.30 p. m.	1	126	127	29	12.00 m.	104	84	188
10	3.15 p. m.	0	178	178	May:				
11	12.00 m.	0	200	200	1	3.00 p. m.	118	116	234
12	1.30 p. m.	0	230	230	3	3.00 p. m.	30	186	216
13	12.30 p. m.	1	202	203	5	11.30 a. m.	9	158	167
14	1.30 p. m.	3	237	240	7	1.30 p. m.	0	82	82
15	2.00 p. m.	2	185	187	10	10.00 a. m.	0	8	8

These figures give a total of 582 perfect flowers and 3,640 staminates, or a grand total of 4,222.

DISTRIBUTION OF PERFECT FLOWERS ON THE PANICLE.

When only a small number of perfect flowers are produced, as in such varieties as the Mullgoa, Kistapal, and Salamar, in which 5 to 50 have been counted on one panicle, these flowers usually are produced upon the apex of the main axis of the panicle, with often a few upon the uppermost lateral branches. As the proportion of perfect flowers increases they are found farther down upon the panicle, and in many varieties they occur even upon the lowest lateral branches,

though it is very common for the lower laterals to produce nothing but staminate flowers and the perfect flowers to be limited to the laterals on the upper half of the panicle.

SUMMARY.

Attacking the problem of mango sterility from several angles, as herein outlined, it has been possible to eliminate several factors heretofore generally believed to have some bearing on the question. Apparently the difficulty is not due to any morphological defect in the pollen or to defects in the mechanism of pollination. By the exclusion of these factors and from the observation of trees in Florida and other regions during several seasons, the conclusion has been reached that the problem is a physiological one, connected with nutritional conditions as influenced by changes in soil moisture and food supply, principally the former. While such factors as lack of pollinating insects and loss of pollen through excessive rains may at times have an injurious effect upon the mango crop, it seems safe to assert that the question of pollination is of comparatively little importance from a practical standpoint. Experiments have been undertaken, with the cooperation of Prof. E. J. Kraus, to test the practicability of inducing the formation of flower buds through ringing, girdling, and banding the limbs with wire. The work of Prof. Kraus at the Oregon Agricultural Experiment Station [1] with pomaceous fruits has suggested various methods of this nature, and the results of these experiments with the mango will be watched with interest. At various times excellent results have been reported from ringing and girdling the mango, but systematically arranged experiments along this line have not been undertaken. It may be that ringing the mango should become a standard orchard practice, but it is hoped that from the present experiments it will be possible to learn more concerning the physiology of fruit setting in the mango and thereby establish other orchard practices, such as cultivation or pruning, best adapted to insure commercial crops of fruit. In Cuban experiments, fertilizers very rich in potash have yielded good results in the way of increased fruit production. It is to be hoped that such experiments as these will bring to light a practicable method of encouraging the formation of fruit buds on soils or under climatic conditions which normally tend to produce vegetative growth to the exclusion of reproduction.

[1] Kraus, E. J. The study of fruit-buds. *In* Oreg. Agr. Exp. Sta. Bul. 130, p. 12–21, fig. 15–23. 1915.

WASHINGTON : GOVERNMENT PRINTING OFFICE : 1917